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Richness and Composition of Ground-dwelling Ants in Tropical Rainforest and Surrounding Landscapes in the Colombian Inter-Andean Valley

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Abstract

Tropical rainforests are characterized by having high structural complexity, stratification, and species diversity. In Colombia, tropical rainforests are critically endangered with only 24% of their area remaining. Forest fragments are often valued based on the presence of vertebrate taxa despite that small habitat remnants may still harbor diverse invertebrate communities. We surveyed the ant fauna associated with rainforest fragments and their surrounding landscape elements (including mature forests, flooded forests, gallery forests, live fences, and pastures) in the Magdalena River watershed. Pitfall traps and litter samples were used to estimate ant richness and diversity, and to compare ant composition among landscape elements. We found 135 species from 42 genera, representing 16% of the species and 43% of the genera known for Colombia. Our surveys also uncovered 11 new ant records for the Colombian inter-Andean region and 2 new records for the country of Colombia: *Mycocepurus curvispinosus* (Mackay) and *Rhopalothrix isthmica* (Weber). The highest species richness was found in forest-covered sites, and richness and diversity was lower in the disturbed landscapes surrounding the forest patches. Species composition varied significantly between all habitat types, but was most similar between forest types suggesting that a loss of structural complexity has the greatest effect on ant communities. Across our study sites, ten species showed the greatest response to habitat type and could qualify as indicator taxa for this region. We conclude by discussing the value of conserving even small forests in this landscape due to their ability to retain high diversity of ants.

Introduction

Human activities have modified the environment to such an extent that most landscapes are now mosaics of human settlements, agricultural land, and small fragments of remaining natural areas (Foley *et al* 2005). This transformation of natural ecosystems results in a loss of diversity (Haddad *et al* 2005), the introduction of non-native species (Suarez *et al* 1998), and ultimately changes in community composition and biotic homogenization (Solar *et al* 2015). Habitat loss has been especially aggressive in tropical ecosystems (Etter *et al* 2006). Tropical forests, for example, cover less than 7% of the earth's surface yet contain more than half of terrestrial biodiversity (Corlett & Primack 2010). To document and preserve diversity in tropical ecosystems, research focuses not only on species richness and turnover in remaining forest patches but also in the variety of landscape elements that are a consequence of human activities in these landscapes (e.g., Perfecto *et al* 2007; Philpott *et al* 2010).

In Colombia, tropical rainforests are located below 1000-m elevation and were once widespread in the Amazon, Pacific, and inter-Andean regions. Deforestation has been particularly severe in inter-Andean regions where rainforests are largely restricted to the lower slopes of mountain ranges and along rivers (Opepa 2013). The Magdalena River landscape, for example, consists of lowland tropical rainforest, pre-montane forest in the foothills of the Central and Eastern Andean mountains, and gallery forest along rivers and swamps (Etter 1998). The rainforest ecosystem of the middle watershed of the Magdalena River is considered one of the most threatened and least-protected environments of Colombia (Fandiño-Lozano & van Wyngaarden 2005; Etter *et al* 2006). Excluding wetlands, its original area of about 14,000 km^2 has been severely developed and currently only between 10 and 15% of the forest remains (Etter *et al* 2006). This habitat loss is primarily the result of agriculture, grazing cattle, mining, logging, oil extraction, and a lack of economic alternatives for communities that rely on natural resources (WWF 2001; Stattersfield *et al* 1998). Given the urgency of identifying areas to prioritize conservation in Colombia, a number of studies have estimated the diversity of vertebrate groups in rainforest relics in the middle watershed of the Magdalena River (Hernández-Camacho *et al* 1992; Cuartas & Muñoz 2003). However, the arthropod fauna has largely been neglected from these efforts despite their importance as bio-indicators of habitat disturbance or management (Andersen 1997; McGeogh 1998; Longcore 2003; Uehara-Prado *et al* 2009; Gerlach *et al* 2013), and for informing reserve design (Kremen *et al* 2005).

Ants are often used as indicator taxa for ecological surveys because they are relatively easy to sample (Alonso 2000), are ecologically dominant in most terrestrial ecosystems, and play diverse roles related to food web structure and ecosystem function by acting as predators, prey, scavengers, mutualists, herbivores, and soil engineers (Hölldobler & Wilson 1990; Folgarait 1998; Bluthgen *et al* 2003; Frouz & Jilkova 2008). Knowledge of ant diversity and its distribution can provide insight into the structure of ecological communities (Yanoviak & Kaspari 2000; Sanders *et al* 2003; Lach *et al* 2010). Additionally, ant communities respond rapidly to environment change (Andersen *et al* 2002). Their sensitivity to environmental perturbation, combined with their functional importance and ease of sampling, makes ants ideal taxa for monitoring changes in ecosystems (Alonso 2000; Andersen & Majer 2004; Yeo *et al* 2016) and for evaluating the contribution of different landscape elements to regional patterns of diversity (Perfecto *et al* 2007; Philpott *et al* 2010).

In this study, we sampled the ant fauna associated with the tropical rainforest ecosystem of the Colombian inter-Andean valley. Due to the heterogeneous landscape that remains in this area, we used our surveys to assess the effect of disturbance and land use on ant community composition in six landscape elements that vary in habitat type and level of disturbance: mature forest, flooded forest, gallery forest, live fence, and pasture. Additionally, we used indicator species analysis (Dufrêne & Legendre 1997) to evaluate habitat-specific associations of key ant species.

Ground-dwelling ant communities are sensitive to habitat loss and transformation, particularly in tropical ecosystems (Vasconcelos 1999; Philpott *et al* 2010). Subsequently, we used our surveys to test the hypotheses that (1) landscape elements with lower levels of disturbance (e.g., mature forest) retain greater species richness than more disturbed elements (i.e., gallery forest, pastures, live fences), and (2) that each landscape element maintains a unique assemblage of ants with some conservation value (Silva *et al* 2007; Achury *et al* 2012). We also tested the prediction that the most diverse landscape elements will have the highest number of indicator species (Ribas *et al* 2012). Our results provide justification for surveying, monitoring, and conserving isolated forest fragments and other features of disturbed landscapes based on their unique contribution to the invertebrate fauna of a region.

Methods

Study area

Located in the central part of Colombia, the study area corresponds to the inter-Andean floodplain formed by the middle watershed of the Magdalena River, in the municipality of Yondó in the Antioquia State (Fig 1). The average altitude is 300 m, and the climate is typical of tropical rainforests with an average annual temperature slightly above 30°C and an average of annual precipitation of 4000 mm. This rainfall is distributed in two periods, between March and June, with a peak in April and May, and from September to December, with maximum rainfall between October and November (Castaño-Uribe 2003).

We sampled along 18 transects distributed across six landscape elements: two mature forests (eight transects), floodplain forest (four), gallery forest (two), live fences (two), and pastures (two). The mature forest is composed of two fragments (forests Javas and Bartolo) with areas of 1041 ha (Javas) and 458 ha (Bartolo) and four transects were located in each fragment. The floodplain forest has an area of 210 ha and also housed four transects. The gallery forest and live fence (defined as a row of trees and vegetation left to act as a natural barrier between pastures) spread linearly throughout the study area and each had two transects.

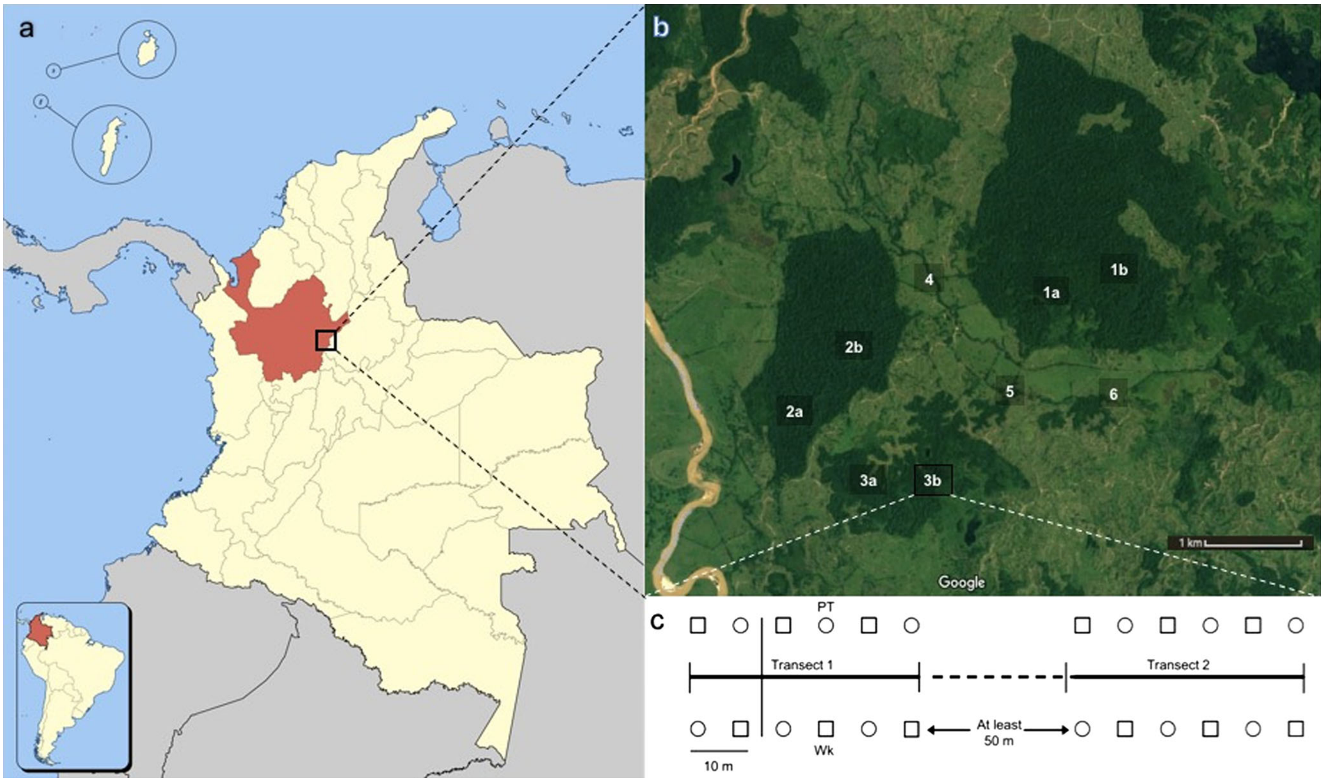

Fig 1 **a** Map of the study area and **b** location of landscape elements chosen for the characterization of ant fauna (Google Inc. 2017): 1—Bartolo forest (74°22′44.98″W, 6°41′3.79″N); 2—Javas forest (74°19′50.28″W, 6°42′8.76″N); 3—flooded forest (74°22′17.70″W, 6°41′11.25″N); 4—gallery forest (74°21′35.32″W, 6°42′20.33″N); 5—live fence (74°20′58.66″W, 6°41′49.05″N); 6—pasture (74°21′24.14″W, 6°41′56.71″N). **c** Schematic representation of transects for ant sampling (PT = Pitfall trap; Wk = 1 m^2 litter sample).

Finally, two transects were placed in pasture which made up the matrix that the other landscape elements were imbedded in (Fig 1). The forests contain vegetation typical of this ecosystem with large trees having a DBH close to 1 m, a canopy of 30 m, and emergent trees exceeding 40 m. The main tree species found in these forests include "barrigón" (*Pseudobombax septenatum*: Malvaceae), "cow tree" (*Brosimum utile*: Moraceae), "fine-leaf wadara" (*Couratari guianensis*: Lecythidaceae), "glassywood" (*Astronium graveolens*: Anacardiaceae), "yellow mombin" (*Spondias mombin*: Anacardiaceae), "Colombian mahogany" (*Cariniana pyriformis*: Lecythidaceae), "pouteria trees" (*Pouteria* sp.: Sapotaceae), "kapok" (*Ceiba pentandra*: Malvaceae), "trumpet tree" (*Cecropia peltata*: Urticaceae), and "shimbillo" (*Inga* spp.: Fabaceae).

Ant sampling

We conducted field work during Colombia's rainy season in December 2012. Ants were collected using two well-established methods for ant surveys (Agosti *et al* 2000): pitfall traps and mini-Winkler extractions. Pitfall traps consisted of 250 ml plastic cups, 10 cm in diameter, which were placed on the ground with the lip of the cup flush with the soil. Pitfall traps contained a solution of 70% alcohol and were collected after 24 h. The mini-Winkler method consisted of sifting 1 m^2 of litter, placing the litter into a mesh sack, and hanging the sack in a Winkler bag for 48 h. During this time, arthropods fell into a collecting bottle with 80% ethanol at the bottom of the bag.

Each of the 18 transects was 50 m in length and contained six sampling stations, consisting of a pitfall trap and litter sample at each station, placed 10 m apart (Lozano-Zambrano *et al* 2009). Transects located in the same landscape element were located at least 50 m apart. This method was proposed by the Humboldt Institute, which is the entity in charge of the biodiversity inventories in Colombia, and it has been used across environments in Colombia in order to produce ant inventories (e.g., Villarreal *et al* 2004; Herrera-Rangel *et al* 2015). This design resulted in a total of 108 sampling stations with a pitfall trap and litter sample at each. After samples were collected, ants and other invertebrates were separated from debris in the laboratory. All specimens were preserved in 95% ethanol. Ants were identified to genus using Palacio and Fernández (2003) and to species using a variety of sources including AntWeb (2015 and references within) and Longino's ants of Costa Rica (2009). Additionally, some species were compared with identified vouchers at the Museum of Entomology at the Universidad del Valle (MEUV). A reference collection of material from this study was deposited in MEUV.

Data analysis

Due to limitations in the availability of independent landscape elements at our site (as well as their connectivity), we were not able to sample replicates of all habitat types. Instead, we treat each site as unique and compare species richness among landscape elements in three ways: the total observed number of species, the estimated number of species (based on species accumulation curves), and the average number of species captured per sampling station. These later two methods take into account our unequal sampling effort. We calculated the number of species for each sampling station (one pitfall and one mini-Winkler) and used sampling station as the unit of replication for generating species accumulation curves and richness estimators for each landscape element (Colwell 2013). Sampling effectiveness was estimated using the non-parametric estimator Jack 1. Due to the difference in the number of sampling stations between landscape elements, we compared richness among sites using rarefaction curves (Gotelli & Colwell 2001) in the program EstimateS v.8.2.0 (Colwell 2013). We also calculated diversity using the exponential Shannon index *Exp* ($H' = \sum_{n=1}^{s}(p_i \log p_i)$), where *pi* is the proportion of workers of the species *i* and *s* the total number of species; this index represents the number of equally likely species needed to produce the given value of the diversity index (Jost 2006). To examine differences among sampling elements, we also corrected for multiple comparisons with a Bonferroni test (Gotelli & Ellison 2004).

We examined the similarity of ant assemblages among sites with hierarchical cluster analysis (McCune & Grace 2002). We compared the groups formed using the nonparametric multivariate technique multi-response permutation procedure (MRPP) based on 1000 permutations using the program PC-ORD version 4 (McCune & Mefford 1999). MRPP tests the hypothesis of no difference between two or more pre-defined groups (McCune & Grace 2002). MRPP values were calculated by measuring Bray-Curtis distance of capture frequency data of species.

Finally, we measured the degree of association of ant species with each habitat type using indicator species analysis (Dufrêne & Legendre 1997). This technique generates indicator values ranging from 0 to 100. We assessed the statistical significance of the maximum indicator value for each species using a Monte Carlo test in which the abundance of species between habitats were randomized (1000 iterations) (McCune & Mefford 1999; McCune & Grace 2002).

Results

Ant diversity—general patterns

We captured 135 ant species belonging to 42 genera and 7 subfamilies (Table 1). Seventy percent of the taxa (92 of the 135 species) were identified to species; the remaining 43 species were identified to morphospecies and mainly belonged to megadiverse genera whose taxonomy is not well known. Among these genera, *Pheidole* (26 species) and *Solenopsis* (8) represented 24% of the morphospecies. The most diverse subfamily was Myrmicinae with 69% of the species, followed by Ponerinae with 11%. The genera with the highest number of species were *Pheidole* (27), *Strumigenys* (14), *Solenopsis* (12), and *Rogeria* (7).

Of the 135 species, six were found in all landscape elements (*Nylanderia steinheili* (Forel), *Pheidole* sp. 3, *Solenopsis* sp. 1, *Solenopsis* sp. 2, *Monomorium pharaonis* (Linnaeus), and *Odontomachus bauri* (Emery)), while 54 species were unique to a single element (Table 1). The floodplain forest had 15 exclusive species, followed by Bartolo forest (13) Javas forest (11), live fence (10), gallery forest (4), and pasture (1). Many of these species exclusively associated with forests are characterized as habitat or prey specialists belonging to the following genera: *Carebara*, *Stegomyrmex*, *Leptogenys*, *Proceratium*, *Xenomyrmex*, and some *Gnamptogenys* and *Pachycondyla*.

Two of the species captured are new records for the country of Colombia: *Mycocepurus curvispinosus* (Mackay) and *Rhopalothrix isthmica* (Weber). In addition, 11 species are new records for the Antioquia State region: *Camponotus bidens* (Mayr), *Carebara striata* (Xu), *Carebara urichi* (Wheeler), *Cephalotes mompox* (De Andrade & Baroni Urbani), *Ectatomma confine* (Mayr), *Leptogenys pubiceps* (Emery), *Leptogenys ritae* (Forel), *Megalomyrmex cuatiara* (Brandão), *Neoponera curvinodis* (Roger), *Pachycondyla conicula* (MacKay & MacKay), and *Proceratium micrommatum* (Forel). A few other species, while not new records, are rarely collected (e.g., *Stegomyrmex manni* (Smith), *Discothyrea horni* (Menozzi),

Table 1 List of ant species collected in the tropical rainforest of Colombian inter-Andean valley. *W* Winkler-sack, *P* pitfall trap, *B* Bartolo forest, *F* flooding forest, *J* Javas forest, *G* gallery forest, *L* live fence, *P* pasture.

Taxa	Method	Landscape element
Dolichoderinae		
Azteca chartifex (Emery)	W	J
Dolichoderus bispinosus (Olivier)	P, W	B, F, L
Dolichoderus lutosus (Smith)	P	L
Linepithema cf. *aztecoides*	P, W	G, L
Linepithema fuscum (Mayr)	P	P
Ectatomminae		
*Ectatomma confine**	P	B, J
Ectatomma ruidum (Roger)	P, W	B, J, G, L, P
Ectatomma tuberculatum (Olivier)	P	G
Gnamptogenys haenschei (Emery)	P	B
Gnamptogenys mecotyle	W	F
Gnamptogenys minuta	W	B, F
Gnamptogenys striatula (Mayr)	P, W	B, J, L
Gnamptogenys sulcata (Smith)	P	F
Typhlomyrmex pusillus (Emery)	W	B, J
Formicinae		
Brachymyrmex heeri (Forel)	P, W	F, L, P
Brachymyrmex longicornis (Forel)	W	B, J, G, L
Brachymyrmex sp. 1	W	F
*Camponotus bidens**	P, W	L, P
Camponotus cf. *bretessi*	P	F
Camponotus sp. 1	P	L
Camponotus sp. 2	W	L
Nylanderia sp. 1	P	J
Nylanderia steinheili	P, W	B, F, J, G, L, P
Myrmicinae		
Apterostigma pilosum (Mayr)	W	B, L
Atta colombica (Guérin-Méneville)	P, W	B, F, J, G, L
Carebara brevipilosa (Fernández)	P	B
*Carebara striata**	W	F
*Carebara urichi**	W	B
Cephalotes atratus (Linnaeus)	P	B
*Cephalotes mompox**	P	B
Cephalotes umbraculatus (Fabricius)	P	L
Crematogaster carinata (Mayr)	P, W	F, J, L
Crematogaster distans (Mayr)	W	L, P
Crematogaster erecta (Mayr)	P, W	B, J, L, P
Crematogaster flavosensitiva (Longino)	W	B, F, J
Cyphomyrmex costatus (Mann)	P, W	B, F, G
Cyphomyrmex minutus (Mayr)	P, W	B, J
Cyphomyrmex rimosus (Spinola)	P, W	B, F, G, L
Hylomyrma reitteri (Mayr)	P, W	B, F, G, L
*Megalomyrmex cuatiara**	W	J
Megalomyrmex silvestrii (Wheeler)	P, W	B, J, L
Monomorium pharaonis	P, W	B, F, J, G, L, P
*Mycocepurus curvispinosus***	P, W	B, J
Mycocepurus smithii (Forel)	P	G
Myrmicocrypta sp. 1	P, W	B, F, J, G, L
Octostruma balzani (Emery)	P, W	B, F, J, L
Octostruma iheringi (Emery)	P, W	J, L
Pheidole colobopsis	W	J
Pheidole sp. 1	P, W	B, F, J, G, L
Pheidole sp. 2	W	F
Pheidole sp. 3	P, W	B, F, J, G, L, P
Pheidole sp. 4	P, W	B, J
Pheidole sp. 5	W	B, F, J
Pheidole sp. 6	W	J
Pheidole sp. 7	P, W	B, J
Pheidole sp. 8	W	J
Pheidole sp. 9	W	B, J
Pheidole sp. 10	P, W	B, J
Pheidole sp. 11	P, W	B, J
Pheidole sp. 12	P, W	F, J
Pheidole sp. 13	P, W	B, F, J, L
Pheidole sp. 14	W	B, J
Pheidole sp. 15	P, W	B
Pheidole sp. 16	P	B
Pheidole sp. 17	P	B
Pheidole sp. 18	W	B
Pheidole sp. 19	P	F
Pheidole sp. 20	W	F
Pheidole sp. 21	P	F
Pheidole sp. 22	P	F, L
Pheidole sp. 23	P, W	G, L, P
Pheidole sp. 24	W	G
Pheidole sp. 25	P	G
Pheidole sp. 26	W	L
*Rhopalothrix isthmica***	W	B, L
Rhopalothrix weberi (Brown & Kempf)	W	B, J
Rogeria alzatei (Kugler)	W	B, F, J, G
Rogeria besucheti (Kugler)	W	F, J
Rogeria nevadensis (Kugler)	W	L
Rogeria curvipubens (Emery)	W	L, P
Rogeria foreli (Emery)	W	F, J, G
Rogeria gibba (Kugler)	W	B, F, J
Rogeria sp. 1	W	F
Sericomyrmex sp. 1	P, W	B, F, J
Solenopsis altinodis (Forel)	W	B, G
Solenopsis cf. *terricola*	W	B, J
Solenopsis geminata	P, W	B, J, G, L, P
Solenopsis picea (Emery)	P, W	B, G
Solenopsis sp. 1	P, W	B, F, J, G, L, P
Solenopsis sp. 2	P, W	B, F, J, G, L, P
Solenopsis sp. 3	P, W	B, J
Solenopsis sp. 4	P, W	B, F, J, G, L

Table 1 (continued)

Taxa	Method	Landscape element
Solenopsis sp. 5	P, W	B
Solenopsis sp. 6	P, W	F
Solenopsis sp. 7	P, W	F
Solenopsis sp. 8	P, W	G, L
Stegomyrmex manni	W	B
Strumigenys villiersi (Perrault)	W	B, J
Strumigenys deltisquama (Brown)	P, W	B, J, G, L
Strumigenys denticulata (Mayr)	P, W	B, F, J, G
Strumigenys eggersi (Emery)	P, W	B, F, G, L, P
Strumigenys elongata (Roger)	P, W	B, F, J, G
Strumigenys emmae (Emery)	W	L
Strumigenys grytava (Bolton)	P, W	L, P
Strumigenys lanuginosa (Wheeler)	W	B, P
Strumigenys lousianae (Roger)	W	L
Strumigenys marginiventris (Santchi)	P, W	B, J, G, L, P
Strumigenys perparva (Brown)	P, W	B, J, L
Strumigenys spathula (Lattke & Goitía)	W	J
Strumigenys subedentata (Mayr)	W	L
Strumigenys zeteki (Brown)	P, W	B, F, J, L
Tetramorium simillimum (Smith)	W	F
Tetramorium sp. 1	W	B, F, J
Trachymyrmex bugnioni	P, W	B, G
Wasmannia auropunctata (Roger)	P, W	F, G, L, P
Wasmannia sigmoidea (Mayr)	P, W	L, P
Xenomyrmex stollii (Forel)	P	F
Ponerinae		
Anochetus simoni (Emery)	W	B
Hypoponera opaciceps (Mayr)	W	F, L, P
Hypoponera opacior (Forel)	W	B, J, L
Hypoponera parva (Forel)	W	L
Hypoponera sp. 1	W	F, G, L
*Leptogenys pubiceps**	P	J
*Leptogenys ritae**	W	B, J
Mayaponera constricta (Mayr)	P, W	F
Neoponera apicalis (Latreille)	P	J
*Neoponera curvinodis**	P	B
Neoponera verenae (Forel)	P	J
Odontomachus bauri	P, W	B, F, J, G, L, P
*Pachycondyla conicula**	W	B, F, J
Pachycondyla harpax (Fabricius)	P, W	B, F, J, G, L
Pachycondyla impressa (Roger)	P, W	B, F, J, G
Proceratiinae		
Discothyrea horni	W	B, F, J
*Proceratium micrommatum**	W	J
Pseudomyrmecinae		
Pseudomyrmex boopis (Roger)	P	F, J, L

*New record for the Antioquia state.

**New record for Colombia.

Gnamptogenys mecotyle (Brown), *Gnamptogenys minuta* (Emery), and *Pheidole colobopsis* (Mann)).

Species richness across landscape elements

Considering all sampling stations together, our observed species accumulation curve relative to the estimate suggests a sampling effectiveness of approximately 77%. The estimator suggests that, given additional sampling, there may be between 37 and 52 additional species present across our sites. The difference between the observed and predicted richness is likely driven by the difference in number of uniques (15) versus the relatively high number of duplicates (40).

The number of subfamilies collected in each landscape element varied between five and seven (Fig 2). The number of genera detected at each site ranged from 15 (37% of the 42 total genera) in the pasture to 34 (85%) in the Bartolo mature forest (Fig 2). Similarly, ant species richness was highest in the Bartolo forest (74 species) and lowest in the pasture (22 species) (Fig 2). Rarefaction curves revealed differences among sites in estimated species richness ($F_{(5.66)} = 168.98$; $p < 0.001$). Bartolo forest and the live fence had higher richness than the other elements (Tukey: $p < 0.001$), Javas forest had higher richness than floodplain and gallery forests (Tukey: $p < 0.001$), and the pasture had the lowest number of species in these analysis (Fig 3).

In addition to patterns at the site level, we found differences in the number of species per sample station among elements ($H = 38.98$, df = 5, $n = 108$, $p < 0.001$, Bonferroni-adjusted testwise error: $p < 0.05/6 = 0.008$) (Fig 4). Relative to other landscape elements, species number per station was highest in the Bartolo forest (median number of species: 14), live fence (14), and Javas forest (11), and each had more species per station than floodplain forest (6.5) and pasture (5.5). In contrast, gallery forest (10) was not different to any of the other elements (Fig 4).

Examining diversity among elements based on the first-order diversity index (Exponential Shannon index e^H) the Bartolo forest was the element with the highest diversity (43.19), and on average, the Javas forest (39.96), floodplain forest (40.69), and live fence (40.85) contained about 93% of the diversity harbored by the Bartolo forest. The gallery forest (27.77) contained 64% of diversity of Bartolo forest, and the pasture (15.97) was the element with the lowest Shannon diversity value, being almost three times less diverse with only 36% of the diversity of the Bartolo forest.

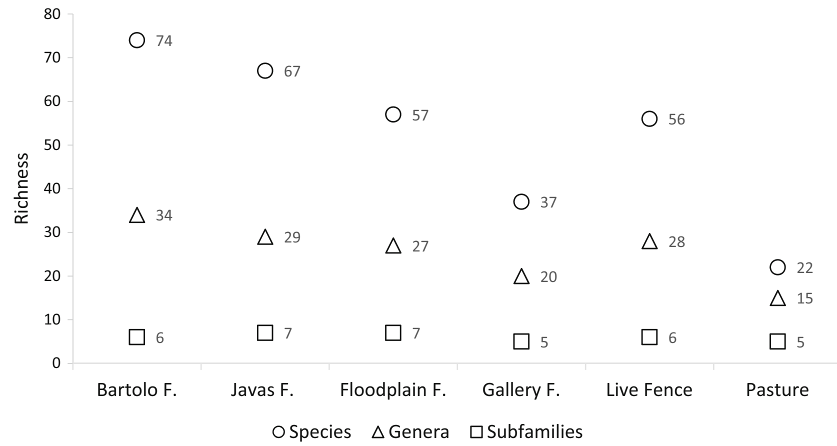

Fig 2 Richness of subfamilies, genera, and species of ants captured in six landscape elements of tropical rainforest in the middle watershed of Magdalena River.

Species composition and indicator species

We evaluated differences in species composition using a dendrogram and found three distinct groups of sites differentiated with a level of retention over 50% (Fig 5). The first group consisted of Bartolo and Javas forests, the second included floodplain forest and gallery forest, and the third group included the live fence and pasture. The three groups differed significantly in species composition (*MRPP*: $A = 0.094$, $T = 5102$, $p = 0.0001$).

Ten species had strong associations to individual landscape elements with indicator values between 54 and 89 (Table 2). Three species were associated with Javas forest, one with floodplain forest, two with gallery forest, three with live fence, and one with the pasture. Four indicator species belonged to the species rich genus *Pheidole*. In the gallery forest, one of the indicators was a fungus-growing ant (*Trachymyrmex bugnioni* (Forel)). In the live fence and pasture sites, indicator species were from genera typical of open areas (Table 2).

Discussion

This research represents the first survey of ants of the Magdalena Watershed region of Colombia and reinforces the importance of conserving even small forest remnants due to their ability to retain high arthropod diversity in tropical landscapes. Even with limited sampling, our rapid inventory detected 59% of the subfamilies, 43% of the genera, and 16% of the species known for Colombia (Fernández 2006) and 59, 64, and 53%, respectively, for the Antioquia state (Vergara-Navarro & Serna 2013). We also report two new ant records for the country. Given the limited scale of our sampling, and that it did not incorporate a seasonal component, the richness estimated for this area is undoubtedly underestimated. However, we can still infer the importance of these forest fragments for conservation given the number of species retained and the unique composition of different landscape elements.

We were able to identify 68% of the taxa to species. The remaining morphospecies belonged to highly diverse genera such as *Pheidole* and *Solenopsis* where taxonomic resources are underdeveloped. A few species were found in all our sites

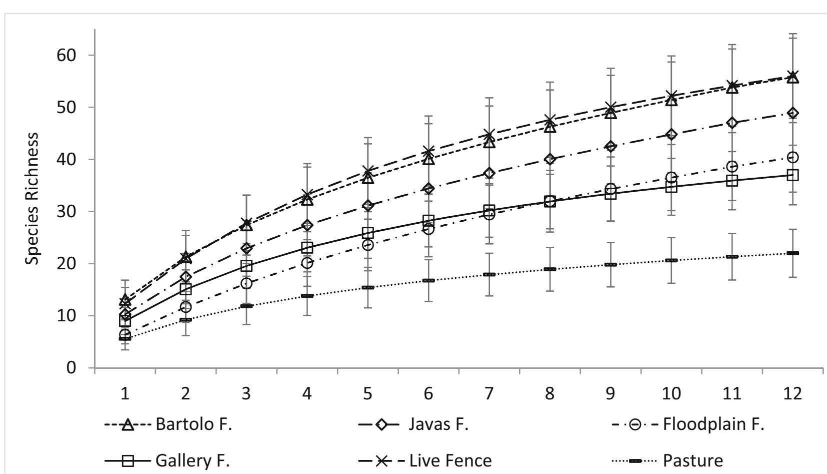

Fig 3 Estimated species richness (with 95% confidence intervals) based on rarefaction curves for six elements of tropical rainforest in Colombia. The 12 intervals on the x-axis represent the fewest sampling stations used in an element.

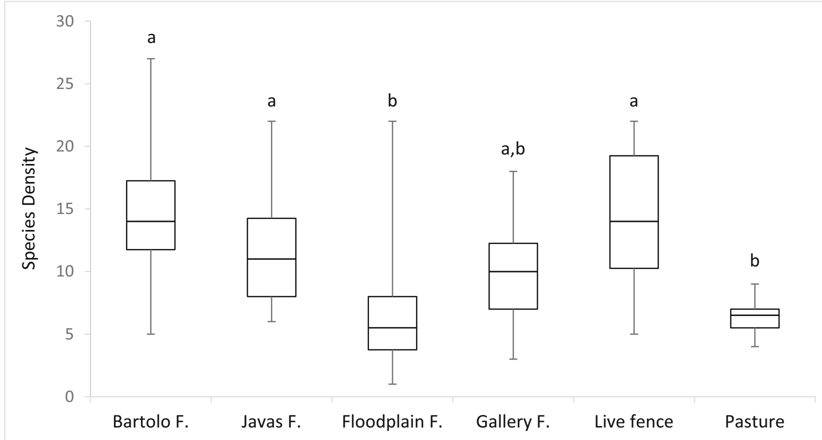

Fig 4 Comparison of the number of species detected per sample station among six landscape elements. Boxes represent 25–75% percentiles and lines extend to upper and lower maximum values per sample within a site. Sites with different letters are statistically different.

and their biology likely reflects general nesting requirements and an ability to persist in disturbed ecosystems. These species include two unidentified thief ants (*Solenopsis* spp.), an undescribed *Pheidole* and the trap-jaw ant *O. bauri*, *N. steinheili*, and *M. pharaonis.* Notably, *M. pharaonis* is recognized as a cosmopolitan tramp species that is common in perturbed and agricultural landscapes worldwide (Wetterer 2010). *Nylanderia steinheili* has been introduced to Africa but is native to the Neotropics including Colombia (Wetterer 2015). Another introduced species that we detected at most sites was the tropical fire ant, *Solenopsis geminata* (Fabricius). While native to parts of central and South America, this species has been introduced globally and increases in abundance in disturbed areas even in its native range (Wetterer 2011; Gotzek *et al* 2015). The presence of *M. pharaonis* and *S. geminata* inside the forests at our sites reflects a high level of perturbation to this ecosystem and its susceptibility to invasion.

Our surveys uncovered two new ant records for the country of Colombia, *M. curvispinosus* and *R. isthmica*. *Mycocepurus* are fungus-growing ants in the tribe Attini (subfamily Myrmicinae) that generally use a variety of organic matter as a substrate for their fungal gardens (MacKay *et al* 2004). *Mycocepurus* is a genus with five described species among which *M. curvispinosus* was previously reported ranging from México to Panama (MacKay *et al* 2004). Meanwhile, *Rhopalothrix* is one of the rarer genera in the Basicerotini tribe (subfamily Myrmicinae). The biology of species in this genus is nearly unknown and species are normally captured only in soil/litter samples (Longino & Boudinot 2013). The geographic range of *R. isthmica* includes Panama, Honduras, and Guatemala (Longino & Boudinot 2013). The distribution of these species now extends south into Neotropical South America and, along with 11 new species we report for this area of Colombia, highlights the importance of this under-surveyed ecosystem.

Fifty-four species were found in a single landscape element and 72% of these species were found in three forest sites (Javas, Bartolo, and flooded forest). However, even the surrounding landscape elements are important for conserving ant diversity given the high species turnover among sites and the unique species that were found in disturbed elements, particularly the live fence. Several studies have shown that forest remnants connected together by live fences or gallery forests retain higher diversity possibly due to landscape heterogeneity and increased movement of species between sites (Cook *et al* 2002; Dauber *et al* 2006). In our study, the sampling stations in live fence had among the highest richness of all sites. This suggests that conserving natural features in disturbed landscapes is valuable for preserving diversity directly in addition to any role they play in increasing connectivity.

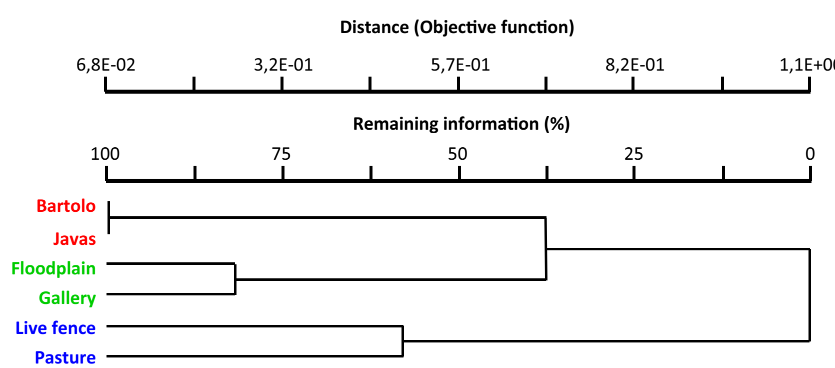

Fig 5 Clustering of the ant assemblages at the six sampled elements, based on the Sorensen (Bray-Curtis) index of dissimilarity and the beta-flexible clustering method ($b = -0.25$). Different colors represent groups formed with a level of retention over 50%.

Table 2 Indicator species analysis (Dufrêne & Legendre 1997) and significance test of Monte Carlo. The values displayed ranging from zero (no indication) to 100 (perfect indication).

Species	Indicator value		Monte Carlo test	Element
	Observed	Expected		
Strumigenys denticulata	63.9	31.3	0.021	Javas
Pheidole sp. 4	63.6	29.2	0.007	Javas
Pheidole sp. 10	54.5	27.9	0.048	Javas
Pheidole sp. 12	75.0	28.4	0.005	Floodplain
Solenopsis sp. 8	83.3	29.8	0.017	Gallery
Trachymyrmex bugnioni	75.0	27.7	0.030	Gallery
Octostruma iheringi	88.9	31.1	0.031	Live fence
Hylomyrma reitteri	73.7	30.6	0.036	Live fence
Pheidole sp. 13	57.1	30.5	0.023	Live fence
Wasmannia sigmoidea	88.9	30.1	0.019	Pasture

Comparing species richness among landscape elements suggests reduced diversity with increasing level of disturbance (from forest to pasture). This pattern is common in tropical areas (Majer *et al* 1997; Carvalho & Vasconcelos 1999, Armbrecht & Perfecto 2003; Silva *et al* 2007) where species richness decreases along a gradient of disturbance or increasing land use. For example, Perfecto *et al* (2007) reviewed 22 studies, 18 of which found ant diversity declined with increasing land use. In the tropics, a large threat is conversion of forest to pasture for cattle raising which can lead to a loss of ant diversity (Philpott *et al* 2010), especially for litter-inhabiting cryptic species and specialized predators (Bestelmeyer & Wiens 1996). Despite the relatively low number of ant species inhabiting pasture, across the landscape as a whole, open areas such as pastures can increase overall diversity by providing open spaces for hot climate specialists and species adapted to disturbance (Bestelmeyer & Wiens 1996).

High beta diversity among sites is common in areas that vary in habitat structure and suggests that habitat heterogeneity is essential for maintaining diversity, even in disturbed landscapes (Stein *et al* 2014; Yeo *et al* 2016). Mechanisms that can explain changes in species composition within and among sites include habitat structure, micro-environmental variables such as soil temperature and moisture, and percent vegetation cover (Philpott *et al* 2010; Tschinkel *et al* 2012). Indicator species analysis revealed that some species were strongly associated with particular elements. These results, along with that of previous research (Bestelmeyer & Wiens 1996; Lawton *et al* 1998; Andersen *et al* 2002), suggest that ants could be valuable as indicator taxa for conservation and tools for rapid inventories.

Our surveys are hopefully only the start of more comprehensive work to document the ant diversity of the middle watershed of Magdalena River and its distribution across the landscape. This unique habitat is not only threatened by current pressures such as cattle ranching, which is a principal economic activity, but is also projected to experience further habitat loss and modification due to several mining and energy projects in this area. We hope our results along with future research will not only contribute to the knowledge of the ant fauna of this ecosystem but will also be used to optimize management and conservation plans in the future.

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